

Mycorrhizal Colonization of Grapevine Rootstocks under Field Conditions

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Mycorrhizal colonization of grafted grapevines was studied during early establishment of an experimental rootstock vineyard to determine rootstock variability forming functional mycorrhizas. Roots of 10 different rootstocks were examined for the presence of arbuscular mycorrhizal (AM) fungi at the end of the second growing season (1998), and at the time of veraison (onset of ripening) of the third (1999) and fourth (2000) growing seasons. The fine root length density (primary roots with intact cortex) increased in 6 of 10 rootstocks over time. Only one rootstock, Riparia Gloire, showed a marked decrease in fine root length density in 2000, when vines carried their first significant fruit crop. AM colonization was generally above 60% of fine root length for all rootstocks, although significant differences due to rootstock and time of sampling were evident. Rootstocks imparting greater vigor to the scion, particularly Ruggeri 140, Kober 5BB, and SO-4, had consistently higher levels of root colonization by AM fungi. The proportion of roots containing arbuscules at veraison declined from 1999 to 2000 in those rootstocks carrying the highest crop loads. While AM colonization of different rootstocks was positively correlated to yield, the proportion of roots with arbuscules was negatively correlated to yield in 2000. Results of this study show that small differences in the ability to form mycorrhizas exist among rootstocks, but other factors, including crop load and soil moisture, have a large influence on root colonization by AM fungi.

Key words: Arbuscules, glomalean fungi, soil moisture, vesicular-arbuscular mycorrhizae, *Vitis*

Grapevines (including *Vitis vinifera*, related *Vitis* spp., and hybrids) are known to form mycorrhizas with arbuscular mycorrhizal (AM) fungi under normal field conditions (Deal et al. 1972, Karagiannidis et al. 1997, Nappi et al. 1985, Possingham and Obbink 1971, Schubert and Cravero 1985). Based on several pot and field studies where AM fungi have been eliminated from soil, grapevines appear to be dependent on AM fungi for normal growth and development (Biricolti et al. 1997, Karagiannidis et al. 1995, Linderman and Davis, 2001, Menge et al. 1983). While in many cases increased growth of grapevines has been related to enhanced P uptake from soil (Biricolti et al. 1997, Karagiannidis et al. 1995, Petgen et al. 1998, Possingham and Obbink 1971), other nutrients including Fe, Cu, and Zn have also been increased by AM fungi in various grapevine cultivars (Biricolti et al. 1997, Karagiannidis and Nikolaou 1999, Petgen et al. 1998). AM fungi might also confer added drought tolerance to grapevines, as observed with numerous annual crop plants (Augé 2001).

Most new vineyards are planted on rootstocks that provide tolerance to the root pest phylloxera. Resistance to nematodes has also been important in rootstock evaluation (Mullins et al. 1992). Little is currently known about the variation that

may occur in the ability of rootstocks to form mycorrhizas. If sufficient variation exists, this information would be important in the choice of rootstock, particularly under conditions of low phosphorus availability or potential drought stress. Rootstocks that are better at forming mycorrhizas may be better suited for grape-growing under phosphorus or water stress conditions that are often encountered by growers.

Differences in root colonization by AM fungi have been observed in grapevine rootstocks in a few controlled studies. Karagiannidis et al. (1995) and Linderman and Davis (2001) found relatively small differences in colonization among Kober 5BB, Richter 110, and 41B or among Riparia Gloire, Kober 5BB, SO-4, 420A, and 101-14 Mgt rootstocks, respectively, in sterilized soils. Shoot growth responses of different rootstocks to mycorrhiza formation were much larger than the associated differences in root colonization in both studies. Alternatively, Bavaresco and Fogher (1996) found only a slight impact of inoculation with *Glomus mosseae* on growth of Pinot blanc grafted to SO-4, 3309-C, or 41B rootstocks, but found large differences in the level of root colonization in unsterilized soil. Karagiannidis et al. (1997) found significant differences in the level of root colonization among Richter 110, Ruggeri 140, 1103 Paulsen, and 41B rootstocks examined after eight years in a field trial. These studies taken together indicate that differences in the ability to form arbuscular mycorrhizas can occur among different *Vitis* rootstocks, but it is unclear whether plant genotype or other soil and environmental variables dictates root colonization by AM fungi. The consistency of rootstock effects over several years is also unclear.

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The goal of this research was to assess the degree of variation to form functional arbuscular mycorrhizas among *Vitis* rootstocks over several years under natural field conditions in Oregon. A second goal was to assess if AM colonization was related to the breeding heritage of *Vitis* rootstocks.

Materials and Methods

Experimental design and field plot management. A grapevine rootstock trial established on a south-facing slope at the Oregon State University Research Vineyard located near Alpine, Oregon was used for this research. The vineyard is 200 m above sea level and receives ~1100 mm rainfall per year during the fall, winter, and spring. Vine rows are oriented on a north-south axis. The experimental rootstock vineyard was planted in late July 1997 on a site at which Merlot was previously grown. Old vines were removed in 1995 and the soil was disced and rotovated. Winter cover crops were planted in fall 1995 (cereal rye, common vetch) and 1996 (cereal rye, common vetch, oilseed radish). Cover crops were mowed in late spring of the following year and incorporated into soil by disking. Dolomite lime was broadcast at a rate of 8 t ha⁻¹ in the spring of 1997 and incorporated into soil by disking. The new vineyard was planted on a spacing of 1.2 x 2.1 m using a randomized complete block design with five blocks. Each of the 10 rootstocks examined were grafted to Pinot noir clone FPMS 2A scion. Each block contained a five-vine replicate set for each rootstock. Vine rows were kept weed-free during the summer by applying glyphosate at the label rate (Roundup, Monsanto, St. Louis, MO) in a 0.6-m-wide strip in the spring of each year.

Soil was a mixture of Bellpine series (Haplohumult) silty clay loam derived from marine, sedimentary parent material and Jory series (Palehumult) silty clay loam derived from igneous material. The average soil pH in water at planting was 6.0. Soil nutrient availabilities (mg kg⁻¹) from 0 to 50 cm depth determined in May 2000 were NH₄ 3.9, NO₃ 2.1, P (bray 1) 12, K 216, Ca 702, Mg 97.2, Fe 21, Mn 5, B 0.3, Cu 0.5, Zn 0.4. Soil organic matter (0 to 50 cm) was 7.1% (loss on ignition).

Irrigation was applied through a drip system once every two weeks during the months of July, August, and September in 1998, 1999, and 2000. In 1999 and 2000, different rates of irrigation water were applied to various blocks in an effort to decrease the variability in vine vigor found at the end of 1998. Irrigation water was applied at the rate of 7.6 to 13.7 L per plant, increasing over this range from the top of the hill (highest vigor block) to the bottom of the hill (lowest vigor block). Irrigation was not available in the first year (1997), and vines received supplemental water by hand. Fertilizer (20-10-20 with micronutrients) was applied with the irrigation water at the rate of 3.6 g per plant during each irrigation event.

All vines were pruned to two buds after the first year (1997) and both canes that developed were not further pruned in 1998. In 1999, vines were head pruned and four buds were retained per vine. In 2000, vines were pruned to eight buds.

Canes were trained upright on a double-Goyot trellis with the training wire at 0.8 m above the ground. Canes were hedged in mid-July in 1999 and 2000 at a height of 2.5 m from the ground. All fruit clusters that developed in 1999 and 2000 were maintained on the vines (no cluster thinning).

Root samples were collected on the following dates: 22 October 1998 (end of second leaf), 25 August 1999 (veraison third leaf), and 22 August 2000 (veraison fourth leaf). Veraison is the stage of development when berries change color and begin to ripen.

Root sampling and mycorrhizal assays. Five soil cores (3-cm diameter) were taken to a depth of 50 cm at a distance of 15 to 20 cm from the base of each vine representing a given rootstock. Soil cores were located within the weed-free zone of the vine row. Cores from each block of five vines were pooled and treated as a single experimental unit. A 50 to 75 g subsample of soil was removed from each sample to determine moisture gravimetrically (Gardner 1986). Soil samples were dried at 110°C for 7 days to obtain soil dry mass. Grapevine roots were hand-picked from the soil, washed over a 500 µm sieve, and separated into two fractions. Woody roots of all diameters were included in a single fraction (class C, D, and E as defined by Mohr [1996]). Small diameter woody roots (1 to 3 mm) were distinguished from fine roots by the loss or collapse of the cortex. Only those woody roots containing a white stele were included. Fine roots were defined as primary roots with an intact cortex varying in color from white to brown (class A and B as defined by Mohr [1996]). Root fractions were blotted dry on paper towels and weighed. The length of woody roots was measured with a ruler. Fine roots were stored in FAA (formaldehyde:acetic acid:alcohol 5%:10%:50% v/v) for up to 2 months before clearing and staining to reveal AM fungi. Roots were cleared and stained by the following treatment: incubated at 90°C in 5% (w/v) KOH for 30 min, rinsed two times with water, incubated at room temperature in 3% H₂O₂ for 30 min, rinsed with water, incubated in 1% HCl at 90°C for 10 min, incubated in stain (0.5% w/v trypan blue, 5% v/v lactic acid, 50% v/v glycerol) at 90°C for 30 min, and incubated in de-stain (5% lactic acid, 50% glycerol) overnight at room temperature.

Fine root length was determined by the grid-line intercept method (Newman 1966) under a stereoscope. AM colonization was determined on randomly selected root fragments using a modified method described by McGonigle et al. (1990). The method was modified by carefully squashing roots mounted in parallel lines between two microscope slides (cover slips were too fragile). The proportion of fine root length colonized by AM fungi was determined at 60 to 300 x under a compound microscope by assessing intersections between root fragments and the eyepiece micrometer at 2.5 mm increments. Roots were considered mycorrhizal if they contained vesicles, arbuscules, coils, or nonseptate hyphae within the cortex at the point of intersection between the root and eyepiece micrometer. A separate account of root intersections containing arbuscules was determined in 1999 and 2000 only. Arbuscules are specialized, ephemeral structures produced

within root cortical cells and are believed to be the site of nutrient exchange between plant and fungus in arbuscular mycorrhizas (Blee and Anderson 1998, Smith and Read 1997). Arbuscules have a short lifespan (5 to 10 days) and disintegrate after this time, while vesicles and hyphae remain intact within roots over an extended period. A minimum of 100 root intersections was examined for a given sample.

The 10 rootstocks examined in this study are summarized in Table 1. Data for both woody and fine root length were expressed per unit mass of dry soil to correct for differences in sample size. Root length density (mm g^{-1} dry soil) was thus obtained, allowing for comparisons with other studies. Data were analyzed by Multifactor ANOVA using a general linear model in StatGraphics version 5.0 (Manugistics, Rockville, MD). The model used included main effects of year (sampling date) and rootstock and their interaction. Block was included as a main effect in the model, whenever significant at 95% confidence. Homogeneity of variances for all variables was tested using Cochran's test. Relationships among root length, AM colonization, and scion vigor were compared using linear correlations (Pearson's r) on mean values for each of the 10 rootstocks. The mean values for scion pruning mass and fruit yield were obtained from M. McAuley and C. Vasconcelos (unpublished data, 1999) or Shaffer (2002).

Results and Discussion

Grafted grapevines grew little in the first year (1997) due to the late planting date. In 1998, rootstock effects on vigor started to become apparent. In 1999, vines carried their first crop averaging $0.41 \text{ kg vine}^{-1}$ (0.7 tons/acre) with an average pruning mass of 75 g (fresh mass) vine^{-1} across the 10 rootstocks examined in this study. In 2000, vines carried an average crop of $1.54 \text{ kg vine}^{-1}$ (2.6 tons/acre) with an average pruning mass of 281 g (fresh mass) vine^{-1} . Of the 10 rootstocks examined, the *riparia x berlandieri* rootstocks Kober 5BB, Teleki 8B, and SO-4, together with Ruggeri 140 (*rupestris x berlandieri*) consistently imparted the greatest vigor to the scion.

Soil moisture was significantly affected by year (as expected due to different sampling months) and by block because of differential application of water (Table 2). Soil moisture was not affected by rootstock (Table 2), suggesting that all rootstocks were growing under similar moisture regimes even though moisture varied by block. As only the upper 50 cm of the soil profile was examined, it is possible that some rootstocks affected soil moisture below 50 cm. Average soil moisture across all rootstock treatments was 0.23 , 0.14 , and $0.12 \text{ g H}_2\text{O g}^{-1}$ soil in October 1998, August 1999, and August 2000, respectively. Soil moisture increased nearly linearly across blocks ranging from 0.12 to $0.17 \text{ g H}_2\text{O g}^{-1}$ soil in 1999 and 0.11 to $0.14 \text{ g H}_2\text{O g}^{-1}$ soil in 2000.

Length and fresh mass of woody roots obtained in samples were highly variable due to the young age of these vines and the chance encounter of large diameter

roots in cores. Woody root length density increased in most rootstocks by 2000, resulting in a significant main effect of year (Table 2). Rootstocks did not affect the length of woody roots within the three years of our study. Woody root length density averaged 0.38 mm g^{-1} dry soil over all rootstocks and sample dates.

Fresh mass of fine roots was less variable than woody roots with respect to sampling error in our samples. A significant interaction between year and rootstock on fine root length density was found (Table 2), due to the large reduction in fine root length that occurred in Riparia Gloire vines in 2000 (Figure 1). Interaction between year and rootstock on fine root length density was no longer significant when Riparia Gloire was removed from the dataset (Table 2). In 1998 and 1999, Riparia Gloire vines had the greatest fine root length density of the 10 rootstocks examined, even though scion vigor was low. Riparia Gloire is well known for imparting low vigor to scions (Howell 1987, Jackson and Schuster 1997, Rives

Table 1 Summary of *Vitis* rootstocks examined in this study.

Rootstock ^a	Parentage	Abbreviation
Riparia Gloire	rip.	Rip
Schwarzman	rip. x rup.	Swz
101-14 Mgt	rip. x rup.	101-14
3309 Courdec	rip. x rup.	3309
Selection Oppenheimer - 4	rip. x berl.	SO-4
Teleki 8B	rip. x berl.	8B
Kober 5BB	rip. x berl.	5BB
Ruggeri 140	rup. x berl.	140
Richter 110	rup. x berl.	110
Gravesac	rip. x rup. x berl.	Gvs

^aRootstocks were grafted to Pinot noir clone FPMS 2A as scion.

Table 2 Results of ANOVA on root and soil variables measured over three years in 10 *Vitis* rootstocks.

Variable measured ^a	ANOVA significance level			
	Year	Rootstock	Block ^b	Year x rootstock
Soil moisture content (% gravimetric)	<0.001	0.738	<0.001	0.284
Woody root length (mm g^{-1} dry soil)	<0.001	0.186	0.598	0.062
Fine root length (mm g^{-1} dry soil)	0.002	<0.001	0.083	0.011
Fine root length w/o Rip. ^c (mm g^{-1} dry soil)	<0.001	0.005	0.159	0.504
Mycorrhizal colonization (% root length)	<0.001	<0.001	0.007	0.268
Arbuscule frequency ^d (% root length)	0.001	0.304	0.014	0.009

^aSamples collected in Oct. 1998 (end of second leaf), Aug. 1999 (veraison of third leaf), and Aug. 2000 (veraison of fourth leaf).

^bIrrigation differentially applied to five blocks, increasing linearly from 7.6 to 13.7 L vine^{-1} in 1999 and 2000.

^cRiparia Gloire removed from dataset.

^dArbuscule frequency determined in 1999 and 2000 only.

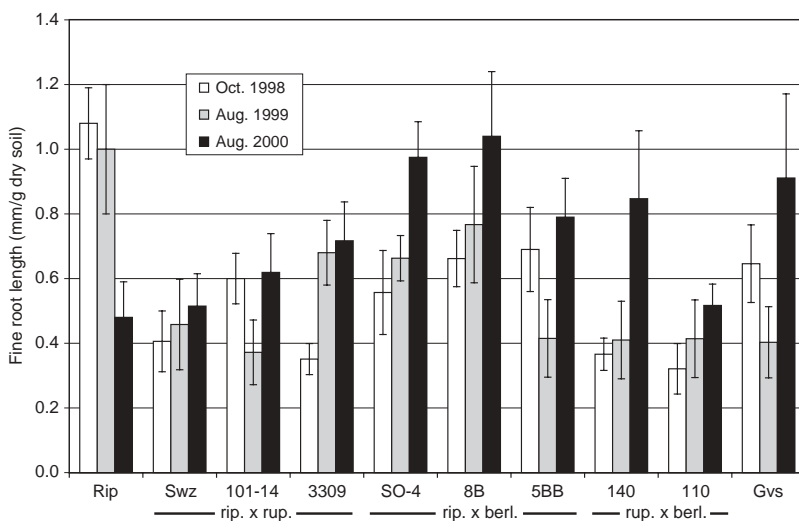


Figure 1 Fine root density (0 to 50 cm depth) of 10 grafted rootstocks over three years in an Oregon vineyard. Values represent means and standard errors of five composite samples. Rootstock abbreviations as in Table 1.

1971). By 2000, Riparia Gloire vines had the lowest fine root density of all the rootstocks examined. It was suspected that this reduction in fine root length was due to increased sink strength of the fruit carried in 2000. Root growth in Riparia Gloire vines appeared to suffer as a consequence of greater photosynthate demand of the fruit. The other rootstocks that imparted low vigor to the scion at this site (Schwarzman and 101-14 Mgt) did not respond in a similar fashion as Riparia Gloire. Both year and rootstock main effects on fine root length remained highly significant after removing Riparia Gloire from the model. Examination of the main effects is thus warranted in the other nine rootstocks.

Fine root length density was significantly affected by year (Table 2), due in large part to the increase of fine roots over time (Figure 1). Six out of ten rootstocks examined showed an increase in fine root density over three years; however, root length of the four remaining rootstocks decreased between 1998 and 1999. One would have predicted that root length would have increased throughout all three years of this study, as vines increased in size and had greater resources to allocate to roots. The observation of reduced fine root length in some rootstocks between 1998 and 1999 can be explained by the later sampling date in 1998. Substantial root growth in grapevines may occur late in the season (Freeman and Smart 1976, Mohr 1996). The quantity of roots obtained at any given point in time results from a balance between root production and root turnover (Comas et al. 2000).

Values for fine root length density were high in comparison to the limited studies reporting fine root length densities in grapevines. Mohr (1996) found an average fine root length of

0.25 mm g⁻¹ dry soil at veraison in 16-year-old Müller Thurgau vines on Kober 5BB rootstock. Smart and Coombe (1983) reported a range of root length density for all root classes of grapevines to be 0.025 to 0.37 mm g⁻¹ dry soil. Fine root length density in this study ranged from 0.32 to 1.08 mm g⁻¹ dry soil. The most likely reason for higher values in this study is the close proximity of the soil cores to the trunks of the vines. Mohr (1996) sampled at a distance of 40 cm from vines. No effort was made here to estimate the average root density for the entire soil profile. Sampling close to vines was necessary to ensure that enough roots would be obtained for an accurate assessment of mycorrhizal colonization. Fine root length densities very close to the value reported by Mohr (1996) were found in a 20-year-old, ungrafted Pinot noir vineyard at the same site as this study when cores were taken from within the vine row and the interrows (R.P. Schreiner, unpublished data, 2000).

Fine root length density was affected by rootstock (Table 2) and rootstock effects were fairly consistent over time after excluding Riparia Gloire (Figure 1). There was a trend for greater root length density to be associated with SO-4, Teleki 8B, Kober 5BB, and Ruggeri 140 rootstocks that imparted more vigor to the scion. Fine root length density was significantly correlated to pruning mass and yield in 2000 (Table 3). Thus, greater scion vigor was related to greater fine root density in this study. A trend between scion vigor and root density determined via the profile wall method was found in comparisons of eight rootstocks (Ramsey, 99 Richter, 101-14 Mgt, 143-B Mgt, Jacquez, 3306-C, De Waal, Teleki) grafted to Chenin blanc (Southey and Archer 1988, Swanepoel and Southey 1989). A correlation between scion

Table 3 Significant correlations (95% confidence) among mean values of root, mycorrhiza, and plant growth variables in 10 *Vitis* rootstocks in 1999 and 2000 (n = 10).

Correlated variables	Correlation coeff(r)	r-Squared	Significance (p)
1999			
Fine root length vs. arbuscule frequency	0.721	0.520	0.019
Mycorrhizal colonization vs. arbuscule frequency	0.651	0.424	0.042
2000			
Mycorrhizal colonization vs. yield	0.853	0.728	0.002
Fine root length vs. yield	0.773	0.598	0.009
Arbuscule frequency vs. yield	-0.769	0.591	0.009
Fine root length vs. pruning mass	0.721	0.520	0.019
Fine root length vs. arbuscule frequency	-0.674	0.454	0.033
Mycorrhizal colonization vs. pruning mass	0.673	0.453	0.033

vigor and root density was not found, however, among AXR1, St. George, and Teleki 5C rootstocks in California (Williams and Smith 1991). It is not known whether the relationship between aboveground vigor and below-ground root growth is driven by a larger canopy capable of providing more assimilates for root growth or by greater root growth providing more water and nutrients for canopy growth.

Mycorrhizal colonization of fine roots was significantly affected by year, rootstock, and block (Table 2). The interaction between year and rootstock was not significant, so that all rootstocks responded similarly over time. Colonization by AM fungi was high in October 1998, declined by veraison 1999, and increased again by veraison 2000 in 9 out of 10 rootstocks (Figure 2). All rootstocks examined had colonization levels above 70% of fine root length by veraison 2000. The trend for colonization to decrease from 1998 to 1999 was probably related to the differences in vine phenology and the timing of root growth. In October 1998, the rate of root growth was likely slowing down, thus allowing for colonization by AM fungi to catch up. AM colonization may have been lower at veraison 1999 because a higher root growth rate at that time of year exceeded the rate of internal spread of AM fungi and/or the rate of initiation of new infection units via AM propagules in soil (Smith and Read 1997). Since colonization increased by veraison 2000 relative to veraison 1999, when root growth rates would have been similar, it can be concluded that either the rate of internal spread of AM fungi in roots had increased or the rate of formation of new infection units had increased. Both mechanisms may have contributed to greater colonization rates in 2000. An increase in the rate of internal spread by AM fungi is likely because plants were larger in 2000 and allocated more resources to roots (indicated by the increase in fine root length density) prior to veraison. An increase in the formation of new infection units is likely also because propagule numbers of AM fungi in the

root zone of the young vineyard would increase over time, having been supported by past root activity.

Rootstock affected AM colonization, resulting in consistently higher levels of root colonization in certain rootstocks (Figure 2). For example, Kober 5BB, SO-4, and Ruggeri 140 had the greatest levels of AM colonization over the three years of this study. The same rootstocks also produced the most vigorous scions at this site. Indeed, AM colonization was better correlated to yield in 2000 than was fine root length density (Table 3). Differences in the level of root colonization within different rootstocks became less pronounced over time. The range of values of AM colonization was much smaller in 2000 than in either year prior, suggesting that all rootstocks might eventually reach a similar, high level of colonization. Nevertheless, these data demonstrate that the choice of rootstock affects AM colonization during the early years of a vineyard.

The range of AM colonization observed in rootstocks of this study (41 to 91%) was similar to other studies conducted in soils ranging from pH 6.2 to 7.6 (Karagiannidis et al. 1995, Karagiannidis et al. 1997) but considerably higher than rootstock trials conducted in calcareous soil (Bavaresco et al. 2000, Bavaresco and Fogher 1996). While differences in AM colonization due to rootstock were evident in all rootstock trials examined to date (including this one), specific rootstocks do not perform consistently across studies. For example, AM colonization in SO-4 was clearly inferior to 3309-C and 41B whenever inoculated with *G. mosseae* in a calcareous soil (Bavaresco and Fogher 1996), but SO-4 was significantly higher than 41B in another study in the same soil (Bavaresco et al. 2000). SO-4 had very high levels of AM colonization in this study. These findings suggest that rootstock effects on AM colonization are influenced by factors other than plant genotype. Examples may include rootstock-scion interactions, scion nutrient requirements, soil fertility, soil pH, or the species of AM fungi present.

Breeding heritage of rootstocks does not seem to be related to colonization by AM fungi. The variation within a similar parentage was just as large as between parent groups in this study. The factors governing mycorrhiza formation in *Vitis* appear to be highly conserved within the genus, but the ultimate level of root colonization by AM fungi appears to be influenced by other variables, including whole plant source-sink relations and soil moisture (see below).

Block significantly affected AM colonization (Table 2). There was a trend for lower colonization to occur in those blocks receiving more irrigation water in 1999 and 2000 (data not shown). AM colonization was significantly correlated to the inverse of soil moisture across all experimental units in 2000 ($r = -0.401$, $p = 0.004$, $n = 50$). Differences in soil moisture similarly affected the proportion of roots with arbuscules (the site of nutrient transfer between plant and fungus). A reduced frequency

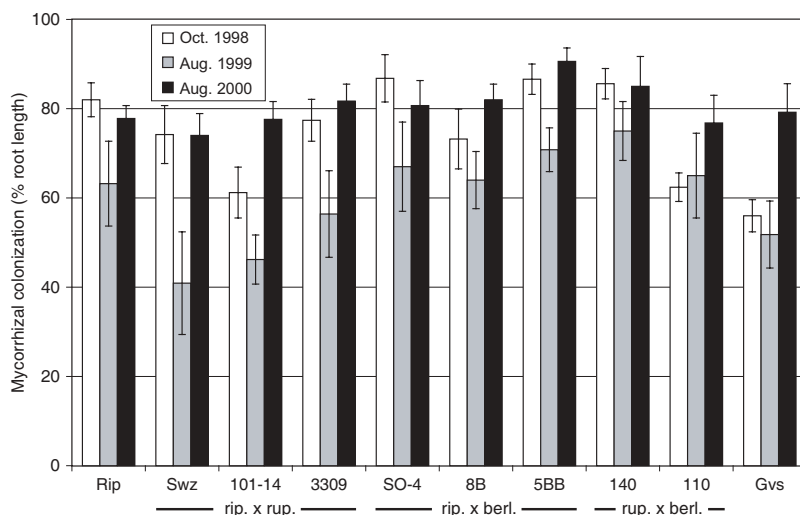


Figure 2 Proportion of fine root length colonized by AM fungi (0 to 50 cm depth) in 10 grafted rootstocks over three years in an Oregon vineyard. Values represent means and standard errors of five composite samples. Rootstock abbreviations as in Table 1.

of arbuscules was found in those blocks receiving more water, and the proportion of roots with arbuscules was similarly correlated to the inverse of soil moisture content across all experimental units in 2000 ($r = -0.390$, $p = 0.005$, $n = 50$). Correlations between soil moisture and AM colonization of roots were evident across the entire data set but could not be examined using the mean values for each rootstock because irrigation was applied at different rates to each block. This is the first observation of reduced colonization by AM fungi in grapevines occurring in response to greater soil moisture. Root colonization by AM fungi has been observed to increase under drier soil conditions in the majority of drought studies conducted with other plant species (Augé 2001).

Crop load appears to be another factor important in determining how mycorrhizal fungi colonize grapevine roots. The proportion of roots containing arbuscules was significantly affected by the interaction between year and rootstock (Table 2). The higher yielding rootstocks (SO-4, Teleki 8B, Kober 5BB, Ruggeri 140) had lower levels of arbuscules in roots in 2000 than in 1999, while the two lowest yielding rootstocks (Schwarzman and 101-14 Mgt) had higher proportions of arbuscules in 2000 than in 1999 (Figure 3). The three highest yielding rootstocks in 2000 had significantly fewer arbuscules in roots compared to the three lowest yielding rootstocks as tested by ANOVA ($p = 0.003$). The average fruit yield of all 10 rootstocks examined was $0.41 \text{ kg vine}^{-1}$ in 1999 and $1.54 \text{ kg vine}^{-1}$ in 2000. The reduction in arbuscules that occurred in those vines carrying the heavier crop load was not due to a lack of AM fungi in the roots, as the total AM colonization was actually higher in 2000 (Figure 2). Rather, arbuscules were specifically reduced in 2000 (Figure 3), as the crop load on vines had increased nearly 4-fold from 1999 to 2000. The average yield for each of the 10 rootstocks examined here was negatively correlated to the frequency of root length with arbuscules in 2000 (Table 3). These results suggest that the greater sink strength of the fruit

in 2000 limited the amount of carbohydrates available in roots for arbuscule formation (Blee and Anderson 1998). Arbuscules are the site of nutrient transfer between plant and fungus in arbuscular mycorrhizas and are likely necessary for the continued production of external hyphae in soil that provide roots with greater absorptive capacity. Thus, the uptake of nutrients or water from soil may be impaired during the time of high fruit demand for photosynthate (veraison-harvest) in vines carrying a heavy crop load because of reduced arbuscules within roots.

Conclusion

This comparison of mycorrhizal colonization among grapevine rootstocks found that small differences in AM colonization were attributed to rootstock genotype, that AM colonization of fine roots and fine root length density were correlated to scion vigor and yield, and that proportion of roots with arbuscules was negatively correlated to yield. These results suggest that colonization by AM fungi may be related to the growth potential of the scion on different rootstocks and that the crop load carried on grapevines may influence nutrient exchange between plant and fungus. Future studies will address the role of mycorrhizal fungi in the nutrition of grafted grapevines.

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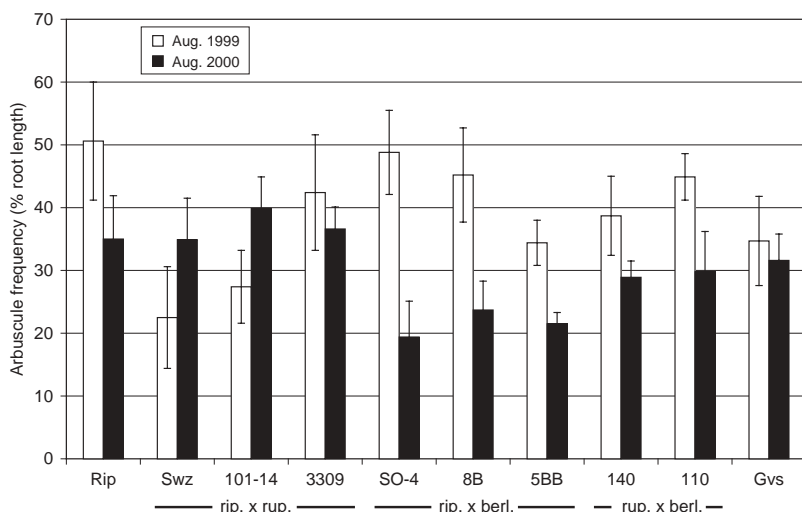


Figure 3 Proportion of fine root length containing arbuscules (0 to 50 cm depth) in 10 grafted rootstocks over two years in an Oregon vineyard. Values represent means and standard errors of five composite samples. Rootstock abbreviations as in Table 1.

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